

On the anatomy and affinities of *Paludestrina ventrosa*, Montague.

By

Guy C. Robson, B.A.

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With 12 Text-figures.

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1. INTRODUCTION.

THE Prosobranch mollusc which is described in this paper is a small insignificant animal found upon plants or bottom débris in the brackish water of creeks and tidal ditches in various parts of England, Wales, and Ireland. It is also found in the upper waters of estuaries. Jeffreys (9) records it from 'the sea coasts of Sweden, France, and Portugal, as well as of Algeria', though such cases are open to a great deal of doubt.

It has been selected for study for several reasons. In the first instance there is very urgent need for more information about the Taenioglossate Prosobranchs to which group the Paludestrinidae are referred. In the second place, though some substantial knowledge is available upon the classification and structure of the Paludestrinidae, the euryhaline habits of

some species of the genus and the general tendency in the group to show a transition from a marine to a fresh-water habit render them a peculiarly interesting group and worth an intensive study. In the last place the recent discovery of Parthenogenesis in *Paludestrina jenkinsi* (Boycott, 4) makes a closer study of the kindred species necessary.

Our knowledge of the European Paludestrinidae includes good accounts of the anatomy and histology of *Bythinella dunkeri* (Bregenzer, 6) and *Vitrella quenstedtii* (Seibold, 20), and more incomplete descriptions of part of the anatomy of *P. ulvae* (Henking, 10) and *P. jenkinsi* (Robson, 16). In spite of this amount of work a good deal remains to be cleared up as to the structure of these animals.

The material employed was obtained from tidal ditches at Leigh-on-Sea, Essex. It was fixed in Bouin's solution after the shell had been carefully cracked away so as to expose the columella. Reconstruction models of various organs were made. A rapid method, which may be capable of improvement, was devised, in which the usual plates were made up of modelling-clay mixed with varying proportions of glycerine and water and rolled out on pieces of thin paper. This mixture can be graded to give a harder medium than Plasticine, and is therefore more suited to making models of such parts as contain delicate ducts, nerves, &c. The paper, if cut larger than the plate, allows of rapid handling and can be cut away after the plate is in position. The surfaces and edges of the plates can be easily painted with water-colours.

The author is indebted to the late Dr. W. G. Ridewood for suggestions as to reconstruction models, and to Professor Paul Pelseneer for information upon the general morphology of the *Taenioglossa*.

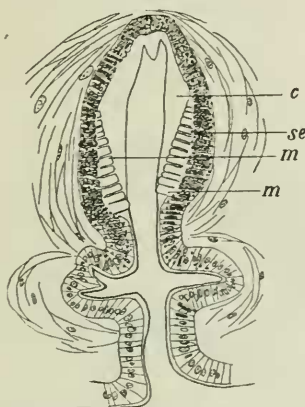
2. STRUCTURE.

1. The Alimentary System.

The oral cavity (Text-fig. 1) is usually deep and narrow. Ventrally it exhibits a pair of lateral diverticula which are sometimes forked. In general it agrees with that of other

members of the genus. It is lined by a cuticle which is fairly thin ventrally, but becomes thicker dorsally. This cuticle is secreted by a columnar epithelium which is continuous with that of the lips and adjacent parts. Each cell of this epithelium contains an elongate, deeply-staining mass of secretion which occupies the major portion of the cell and usually obscures the nucleus. These secretion-masses are especially well developed where the cuticle is deepest; and in these areas the

TEXT-FIG. 1.



Transverse section through the mouth. *c*, cuticle; *m*, mandibles
se, secretory epithelium.

whole epithelium is characterized by a mass of extra-cellular pigment in the shape of very small, subcircular granules.

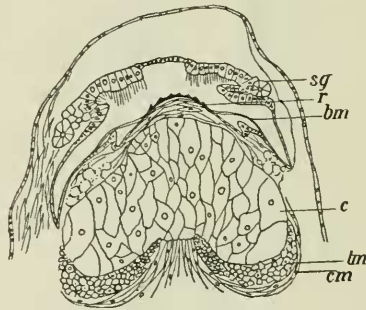
In the upper portion of the mouth is found a pair of mandibles. These consist of a number (minimum 13, maximum 20) of columnar pieces of specialized cuticle, each secreted by a single cell of the basement epithelium, as Seibold found in *Vitrella* (20). That the secretion-masses are intimately concerned in the formation of these is shown by the fact that plates are often continuous with the former. The mandibular plates stain very sharply with eosin, the rest of the cuticle being more or less unaffected by the stain. There is sometimes present, in addition to the mandibles, a specialized piece of

cuticle just below the mandibles on each side. There is also usually a median dorsal projection, dagger-shaped in transverse section. This also stains sharply with eosin, but less intensely than the mandibles.

Behind this projection are to be found at about the same level in the mouth on either side two glandular patches of unknown function which run backwards to the origin of the salivary ducts.

Posteriorly to the mandibles the mouth expands laterally and is flattened dorso-ventrally over the lingual cartilages.

TEXT-FIG. 2.



P. ventrosa. Transverse section through buccal bulb. *c*, oral cartilage; *cm*, circular muscles; *lm*, longitudinal muscles; *bm*, basal membrane of radula; *r*, radula; *sg*, salivary gland.

In this area it shows in transverse section three main divisions—a median, unpaired cavity with a thin roof, dorso-lateral expansions with ciliated and glandular walls into which the salivary ducts open, and ventro-lateral expansions which dip down beside the cartilages. These have a cuticular lining. The cilia of the dorso-lateral cavities no doubt serve to circulate the saliva. In *P. ulvae* Henking considers their function consists in driving the food particles backwards. In *Vitrella* and *Bythinella* the cilia are continued on to the roof of the median portion.

The lingual cartilages (Text-fig. 2) correspond to those found in other genera of the family, and in general to the

excellent description given by Bregenzer for *Bythinella*. They are two somewhat piriform bodies, united dorsally and in the median line. They are rather flattened dorso-ventrally. Posteriorly they diverge somewhat. Bregenzer states that in *Bythinella* they are each divided into a 'Haupt-Knorpel' and a 'Knorpelspange', and regards the difference between *Paludestrina* and *Bythinella* in this respect as of taxonomic value. Certainly no such division is apparent in *Paludestrina ulvae* and *ventrosa*. Lateral expansions ('Flügel') observed in *Bythinella* occur in *P. ventrosa* as well.

The tissue of the cartilages is composed of irregular polygonal cells with relatively small nuclei and a large amount of granular pigment.

It should be noted that Rougemont (18) states that in *Hydrobia* sp. the cartilages are capable of movement upon each other, if pressed downwards. In *Paludestrina*, *Vitrella*, and *Bythinella*, this is, of course, quite possible; as they are no doubt very elastic and have a certain amount of 'play' on each other.

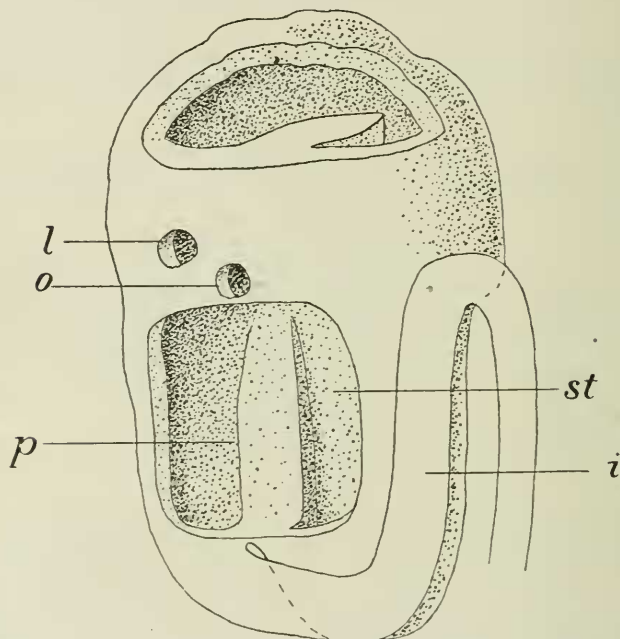
The *radula* has been described and figured by Woodward (24).

The salivary glands are two in number. In *P. ulvae* Henking describes two pairs with separate openings. Those of *P. ventrosa* appear to correspond with Henking's first (larger) pair. They run as far back as do the second pair of *P. ulvae* and sometimes cross over in a similar fashion.

The lateral diverticula of the pharynx disappear posteriorly, and the oesophagus develops a fresh series of diverticula in the form of deep longitudinal furrows. Behind the cerebral commissure the oesophagus in most cases shows a tripartite arrangement as in *Bythinella*. It is ciliated almost up to its distal extremity. The stomach (Text-fig. 3) is an irregularly-shaped organ with a forked appearance exteriorly due to the fact that the intestine and style-sac leave the stomach parallel to each other from its anterior end. The oesophagus and

hepatic duct open into the stomach at its upper (posterior) end. The pyloric part of the intestine and the style sac are in open communication with each other, as in *P. jenkinsi* (Robson, 16), by means of a longitudinal slit for a considerable way. Bregenzer does not refer to this as occurring in

TEXT-FIG. 3.



Diagrammatic reconstruction of stomach to show relationship of crystalline style sac. *p*, pylorus; *i*, intestine; *st*, style sac; *l*, hepatic duct; *o*, oesophagus.

Bythinella. No mention is made by Seibold of a style sac in *Vitrella*, and, as his account is painstaking and thorough, we have to assume that the sac is absent. This is a very curious fact and one to which we shall return later. The oesophagus and hepatic duct open into the stomach fairly closely together. In this region the stomach epithelium is ciliated, the ciliated area being continued downwards and

forwards into the pylorus. On the side of the stomach opposite to the oesophageal and hepatic apertures the epithelium gives rise to a dense cuticle which occupies the major part of the posterior part of the stomach but diminishes anteriorly.

Vitrella and *Bythinella* apparently differ conspicuously in the lining of the stomach. In the latter form only a small part of the stomach is ciliated, while the contrary is true of *Vitrella*. *P. ventrosa* is more or less intermediate between the two in this respect.

The base of the epithelium which secretes the cuticle is, as in the case of the oral cuticle, rendered conspicuous by a layer of densely-staining granules. The stomach is crossed by numerous ridges of which the most constant and most conspicuous is a large and strongly-developed one lying transversely in the cavity above the hepatic duct. Grooves with specialized cuticle are found in the neighbourhood of the latter.

The *style sac* is blunt externally and rather thimble-shaped. In transverse section it is circular and exhibits on the side towards the pylorus a groove of characteristic structure. The latter corresponds in its histological features to the similar structure in *Bythinella*. Bregenzer has offered no explanation of the function of this groove. Unfortunately the structure and relationship of the style itself cannot be demonstrated in fixed material. I am under the impression, however, that, in the living animal, the style is not loose in its sac but attached. If that is the case it may be secreted in the groove.

The rest of the sac is simple, being composed of a thick ciliated epithelium. The cilia are very dense and much longer than the cells.

No one familiar with the recent work on the style sac in Lamellibranchia can fail to be struck with the similarity between the structure here described and that figured by Nelson (14) for *Lampsilis anodontoides*. In both forms the pyloric part of the intestine communicates by a narrow slit with the style sac, the walls of which are composed of a single layer of columnar ciliated cells. In *Lampsilis* the resemblance to *Paludestrina* is still more emphasized by the

presence of a large mass of deeply-staining cells near the slit. In several figures given by Nelson and Edmondson (7) we find a lateral groove like that of *Bythinella* and *Paludestrina*. The similarity between the crystalline style of Gastropods and Lamellibranchs has been commented upon by various authors, and a short discussion may be found in Moore (12).

The pylorus is ciliated and passes gradually into the intestine proper. This follows the usual course. It is ciliated almost to its extremity; a well-marked typhlosole is found extending for some distance down the intestine. This is apparently absent in *Vitrella* and *Bythinella*.

The hepato-pancreas occupies the apical whorls as usual, and consists of branching finger-like processes. The duct is very short and fairly wide. No definite differentiation of the liver-cells into granular- and ferment-cells with different staining and contents could be made out. Vacuoles with inclusions are seen in the plasma of the liver-cells.

The rectum, when viewed transversely, exhibits a number of longitudinal folds. It runs forward in the roof of the pallial cavity projecting from the latter and ultimately becomes free for a short distance.

2. The Nervous System (Text-fig. 4).

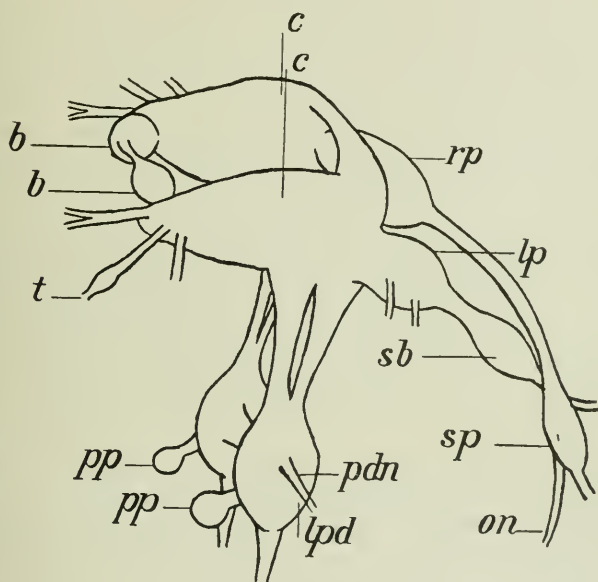
The only description of the nervous system of *Paludestrina* is that of Henking, which is insufficient and leaves a good deal to be desired.

The cerebral ganglia of *P. ventrosa* are long and rather pointed anteriorly. The cerebro-pedal commissure is normal though very short. The buccal commissure calls for some comment as it is extremely short and thus unlike the elongate form found in this and allied families. The buccal ganglia are closely applied to the anterior end of the cerebral ganglia. In one or two cases very short connectives were found; but such instances are rare. Henking does not refer to the buccal commissure as such in *P. ulvae*; but from his description and figure the connectives would appear to be as short as in *P. ventrosa*.

As in allied forms the cerebro-pleural connectives are absent, the ganglia being practically contiguous on each side. The right pleural ganglion is larger than the left. The pleuro-pedal connectives are short and closely applied to the cerebro-pedals.

The pedal ganglia are rather triangular in transverse section. Posteriorly they bear a pair of oteocysts.

TEXT-FIG. 4.



Central nervous system (diagrammatic). *b*, buccal ganglion; *c*, cerebral ganglion; *lp*, *rp*, pleural ganglion; *lpd*, pedal ganglion (*l*); *pp*, propodial ganglia; *sb*, subintestinal ganglion; *sp*, supra-intestinal ganglion; *on*, osphradial nerve; *t*, tentacular nerve and ganglion; *pdn*, parapodial nerve.

The visceral commissure is of the shortened type and resembles that seen in *Vitrella* and *Bythinella*, though it agrees with the former in the amount of abbreviation, the supra-oesophageal pleural connective not being so shortened as in the latter. The supra-oesophageal portion follows the oesophagus more or less closely to the abdominal ganglion

which is situated in the columella region between the kidney and the reproductive organs. The subintestinal portion passes over the surface of the columella muscle to the abdominal ganglion.

Three main nerves are given off from the anterior end of the cerebral ganglia—a large tentacular nerve with a tentacular ganglion and two oral and labial nerves. No separate optic nerve was found, the innervation of the eye being achieved by optic fibres of the tentacular nerve. It may be recalled that Vayssière found that in *Truncatella* (23) the tentacular nerve is apparently responsible for the oculo-motor innervation.

From the left pleural ganglion are given off two nerves of pallial distribution. Each pedal ganglion gives off three main roots—anterior, ventral, and postero-lateral. The first-named always bear at a short distance large and well-defined propodial ganglia. The ventral pair is very stout and sometimes bears ganglia. The postero-lateral pair is very slender and, as in *Bythinella*, sometimes bears a diminutive ganglion. No certain trace of a metapodial commissure was found. It is absent in *P. ulvae* and present both in *Vitrella* and *Bythinella*.

From the supra-intestinal ganglion a nerve passes upwards over the roof of the pallial cavity to the osphradium.

Henking's description of the visceral commissure and its prolongations in *P. ulvae* is in need of correction. Bregenzer, who admits this, is inclined to make taxonomic capital out of his statement that two connectives from the pedal ganglion are found joining the 'Oberschlundganglion', and infers from this that the pleural and cerebral ganglia are completely fused. If this is correct it is difficult to account for Henking's 'accessorische' and 'unpaares' ganglia unless we call these respectively supra-intestinal, subintestinal and abdominal (!) It seems far more sensible to assume that Henking made a mistake about the point of insertion of the pedal connectives, to call his 'l. accessorische Ganglion' the left pleural and his 'unpaares Ganglion' the subintestinal.

3. Sense Organs.

The statocysts are in close proximity to the posterior surface of the pedal ganglia. The auditory nerve is very difficult to trace, and in a large number of preparations I have only succeeded in finding one in which it is clearly seen. It runs backward from the statocyst in close proximity to the cerebro-pedal connective and ultimately becomes indistinguishable from the latter. The cysts contain each a single moderately-sized otolith.

In certain other Taenioglossa, e.g. *Valvata* (Bernard, 1), *Melania* and *Paludina* (Pelseneer, 15), numerous small otoconia replace the single otolith of *Paludestrina*, *Vitrella*, and *Bythinella*. This diversity, which contrasts with the remarkable constancy in the number of otoliths found in Teleostean fishes, might well supply a subject for independent study both from the taxonomic and the physiological point of view.

The cysts are formed of an external layer of very thin epithelium covering an internal layer of irregularly-shaped cells. These are flattened and resemble rather those figured by Bernard (1) for *Valvata*.

In *Valvata* Bernard found no cilia, while Garnault (8) observed that in *Cyclostoma* they are very sparsely developed. In *Bythinella* and *Vitrella* they are not referred to. In *P. ventrosa* it is almost certain they are absent. There is quite definitely no ordinary ciliated layer and nothing more on the interior surface than occasional vague clumps of unrecognizable tissue. How the otoliths in this case stimulate the sensory layer is therefore uncertain unless the latter has a general tactile sensibility. In *Valvata* Bernard (loc. cit.) observed a sort of network formed of prolongations from the membrane of the lining cells.

The eyes do not call for special attention. They resemble those figured by Henking for *P. ulvae* in general form, though they differ in the closer approximation of the inner and outer cornea. In *Bythinella* the space between the two corneas is considerable and filled with connective tissue. In

the same form Bregenzer notes no special differentiation of the outer cornea from the adjacent epithelium of the tentacle base. This is not the case in *P. ventrosa*, in which the external cornea is always noticeably thinner.

The osphradium, as in *Vitrella* and *Bythinella*, is a simple ridge-like elevation on the left-hand side of the gill close to the junction of the roof of the pallial cavity with its floor. There are no foliations such as occur in some other *Taenioglossa*. The laterally-disposed pigment cells contain brownish pigment granules. The ciliated and sensory layer overlies a large and elongate osphradial ganglion.

4. The Respiratory and Circulatory System.

(1) Pericardium and Heart (Text-fig. 5).

The pericardium lies on the posterior side of the body-whorl in a superficial position covered only by the body-epithelium. It is placed at the posterior end of the pallial cavity on the left-hand side, and is roughly bounded by the kidney and the extremity of the style sac.

No trace of a reno-pericardial orifice could be found. Seibold was unable to find one in *Vitrella*; nor is it referred to by Bregenzer for *Bythinella*. It occurs in both *Cyclostoma* (8) and *Valvata* (1). The auricle was never found in an expanded condition, so that its general structure cannot be defined. The ventricle is, as usual, thick-walled and muscular, though a thinner-walled portion of varying extent is invariably to be seen.

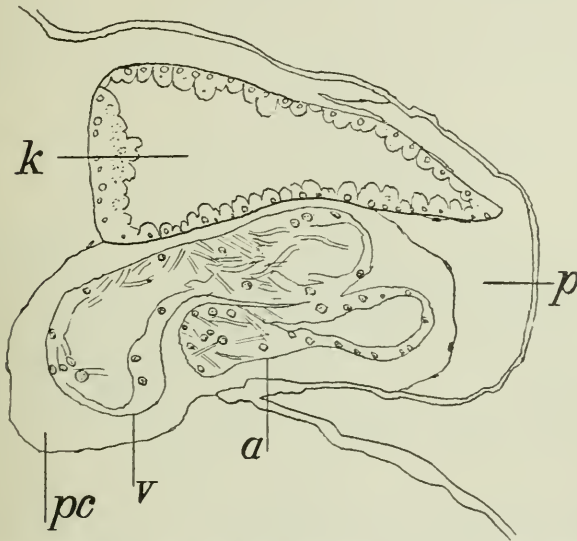
(2) Vascular System.

The descriptions of this system in other *Taenioglossa* are very unsatisfactory. The accounts given are usually incomplete, and frequently omit some portion from consideration. It may also be pointed out that on one point at least two of the most up-to-date treatises on the Mollusca are at variance. Lang (11, p. 322) says, 'Bald öffnen sich die Arterien . . . in arterielle Sinusse. Unter diesen verdient besonders der grosse Kopfsinus . . .' Pelseneer (15), who alludes to the

cavities in which the arteries terminate as 'interorganic lacunae', says (p. 100), 'the venous blood is collected into an anterior or cephalopedal sinus', &c. I share Professor Pelseener's view that the large cephalopedal cavity is venous.

The following outline, which is by no means complete and owing to the size and contractility of the animal is not founded

TEXT-FIG. 5.



Heart, pericardium, and kidney in section. *a*, auricle; *v*, ventricle; *k*, kidney; *p*, portal vein; *pc*, pericardium.

upon injections, may serve to enlarge our knowledge of this system in the *Taenioglossa*.

There appears to be a large general venous sinus of which the chief components (cephalic, pedal, and visceral) are in communication with each other. The two first-named are in open communication posteriorly, but are separated anteriorly by a horizontal septum. Both Henking and Bregenzer speak as though the latter completely separated the two cavities in *P. ulvae* and *Bythinella*. In none of my series, however, is this the case.

From the general venous sinus the blood passes (*a*) to the renal portal system by more or less clearly-defined vessels, (*b*) to the gills through the rectal sinus. From the kidney the blood passes into the portal vein (q.v.). The complete course of the latter is not easy to trace. In one or two cases it was found entering the auricle close to the root of the pulmonary vein, though in other cases its junction is not so clearly seen and it might even open into the pulmonary vein itself. It is possible, however, that some of the blood in the kidney may find its way into the gill directly, as the rectal sinus was adjacent to the kidney on part of its course. The rectal sinus proper appears to be cut off from the other venous sinuses, but to be in communication with them by means of a loose lacunar system.

From the rectal sinus afferent vessels run to the gill and pass along the base of the gill-lamellae (q.v.). The arterialized blood is carried from the gill by the pulmonary vein. It leaves the ventricle by the aorta, which divides into anterior and posterior branches. The first-named runs forward along the wall of the pericardium sending out branches in its course. The posterior branch passes between the stomach and intestine and probably enters a lacuna in this position. From the lacuna is given off among other vessels a clearly-marked genital artery which can be traced backwards to finer branches distributed to the various processes of the gonad.

(3) Respiratory System.

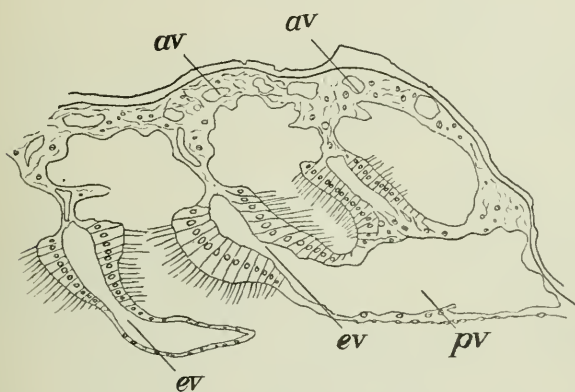
The gill (Text-fig. 6) is monopectinate and composed of broadly-triangular plates hanging freely in the pallial cavity. On the rectal side the extremity of each plate is free for a short distance.

The histology and structure correspond in general with that of *Bythinella*, but Bregenzer does not indicate the relation of the gill to the adjacent parts of the circulatory system.

On the whole it would seem that in *P. ventrosa* the apical portion of the lamellae is more elongate and triangular in transverse section than in other forms. It should be

noted that in this form and *Bythinella* the cilia are not distributed all over the lamellae as in *Vitrella* but are concentrated at the apex. Each plate shows longitudinal folds towards its basal part, becoming flatter where they join up with the efferent vessel. In *Bythinella*, *Vitrella*, and *Paludestrina jenkinsi* the lamellae are flat and unfolded. This folding seems rather difficult to explain. Were it not for the fact that similar folding occurs in *P. ulvae* (Henking) I would be inclined to think

TEXT-FIG. 6.



Gills in section. *av*, afferent vessel; *ev*, efferent vessel; *pv*, pulmonary vein.

that it might be due to shrinkage arising from excessive contraction of the transverse muscles in each filament. But in addition to the occurrence of similar folds in *P. ulvae* there is the fact that, if it were due to shrinkage, one would expect such contraction to take effect over all the lamella, which is not the case. If this ultimately proves to be an invariable character of these two species of *Paludestrina* it may very well be correlated with their brackish-water and marine habitat. It should also be pointed out that unless the text-figures G and H in Bregenzner's paper are diagrammatic the afferent vessels and blood-spaces are much smaller in *P. ventrosa* than in *Bythinella*.

From the rectal sinus blood passes by rather irregular and inconstant lacunar spaces to the roof of the pallial cavity, and finally into more definite and constant lacunae at the base of each gill-lamella. Thence it passes to the afferent vessels, and from these through the blood-spaces in the lamellae to the efferent vessels at the apex of the plates. The efferent vessels of all the lamellae are united on the left-hand margin of the gill by the pulmonary vein. On the left-hand side the afferent vessels apparently lose themselves in lacunae. On the rectal side the efferent vessels come to an end in the free portion of each lamella.

It is probable that blood is brought from the left-hand side of the mantle cavity in a wide irregular lacunar system which ultimately debouches into the same sub-lamellar spaces as the blood from the rectal sinus.

4. Renal System (Text-figs. 5 and 7).

The kidney lies between the body-wall, the pallial cavity, and the pericardium, sending ramifications among some of the other organs as in *P. jenkinsi*. It communicates with the pallial cavity at its own anterior end by a ciliated aperture furnished with sphincter and dilator muscles. In general the kidney is a thin-walled cavity with a lining of special secretory vacuolated cells as figured and described by Bregenzer (6, p. 248). Anteriorly, however, there is a special area between the body-wall and the pericardium characterized by a compact stroma of connective tissue with blood cavities communicating with the portal vein. This is the 'blood-gland' of various authors (cf. Simroth, 21, p. 564). It is present in *Bythinella* but absent in *Paludina*, *Cyclostoma*, and other forms (Simroth, loc. cit.). It is not specifically described in *Vitrella*, and it is not clear from Seibold's description if it actually occurs.

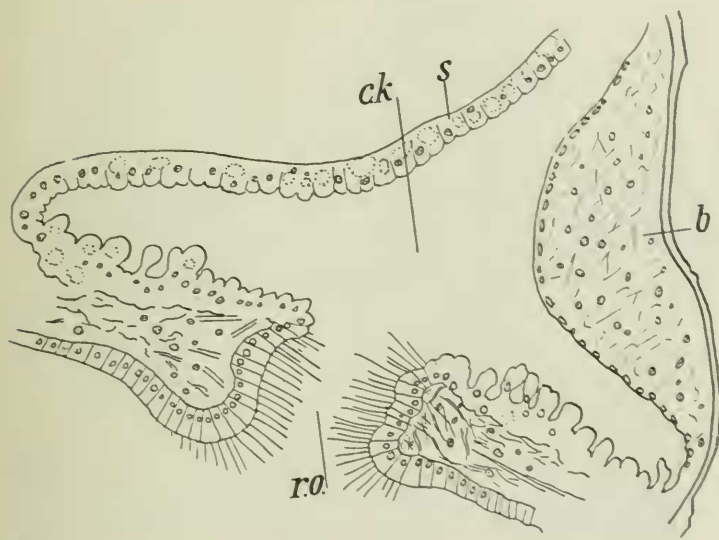
With regard to the epithelium covering this gland on the renal side I do not find the condition described by Bregenzer. The lining is usually a flat epithelium with flattened or roundish nuclei (fig. 7). I have never found the peculiar epithelium figured by Bregenzer (loc. cit., Pl. xvi, fig. 15).

5. Reproductive System.

(1) Female Organs (Text-figs. 8, 9, 10).

The ovary lies as usual between the liver and columella muscle. It consists of branched tubular follicles. The material employed for this study was all collected and preserved during May and June when apparently the oögonia were approaching maturity, but were not being shed in any number. A few

TEXT-FIG. 7.



Renal aperture and 'blood-gland' in section. *ck*, cavity of kidney; *b*, blood-gland; *r.o.*, renal orifice; *s*, secretory epithelium.

were found in the oviduct, and in a small number of cases spermatozoa were found in the receptaculum seminis. It may be therefore considered that, speaking generally, the material examined represented a stage coincident with the beginning of the breeding season.

A great diversity of cellular elements was found in the ovary. The following types were invariably distinguished (Text-fig. 12):

(a) Ripe oögonia distinguished by their large size, large

- yolk content, usually with a clear slightly-granular nucleus and a deeply-staining nucleolus.
- (b) Ovarian cells only distinguished from (a) by the less intense staining of the yolk and their smaller size.
- (c) Small cells of various sizes, free or attached to the epithelium of the follicles with darkly-staining cytoplasm, clear nucleus, and dark nucleolus.

TEXT-FIGS. 8-9.

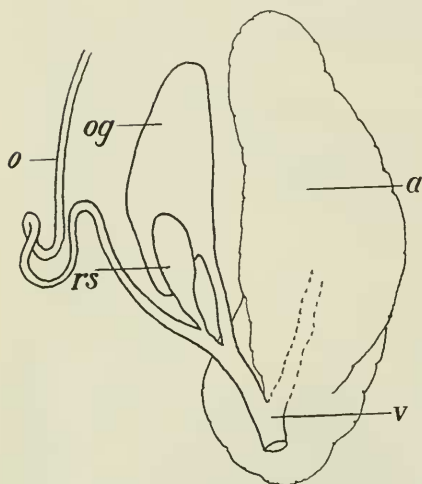


Fig. 8.—Female genitalia. *a*, accessory gland; *o*, oviduct; *og*, oviducal gland; *rs*, receptaculum seminis; *v*, vagina.

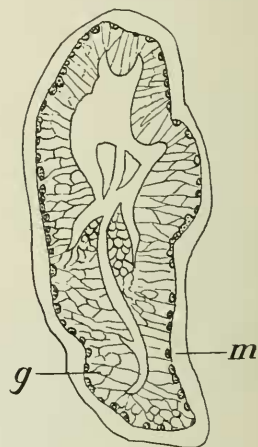


Fig. 9.—Section of oviducal gland. *m*, outer muscular layer; *g*, gland.

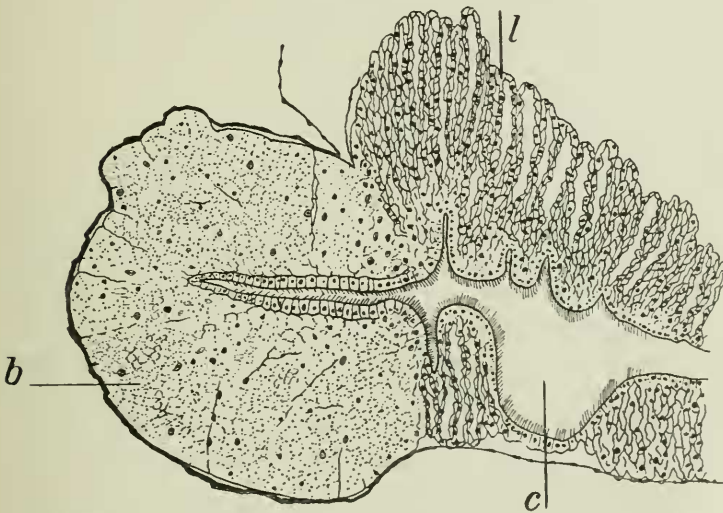
(d) Cells of the germinal epithelium in various stages, either very small and irregular or enlarged and approximating to (c).

The germinal epithelium was never found in the regular columnar condition seen in Bregenzner's figure U; and it is sometimes very difficult to interpret, being full of masses of deeply-staining material of irregular disposition and uncertain nature and often flattened out by the pressure of the ripening oögonia. The various types of ovarian cell with all the intermediate stages are frequently met with in one and the same follicle, and the gradual transition seems to indicate the

development of one main type of cell from the germinal epithelium, viz. oögonia. No traces of nurse-cells could be found.

The oviduct follows the usual course down the columellar region accompanied by the genital artery. It ultimately becomes thick-walled and convoluted. It gives off in succession a receptaculum seminis and an oviducal gland,

TEXT-FIG. 10.



Portion of accessory ♀ glands in section. *b*, darkly-staining area; *l*, purple-staining area; *c*, cavity continuous with vagina.

and opens into the vagina close to the entrance of the accessory glands of the latter. In its upper course its walls consist of a single layer of flattish epithelial cells. In the neighbourhood of the kidney its walls are formed of deeper and more columnar cells which contain at their apices (i.e. towards the lumen) a darkish secretion. They are ciliated and covered by an external layer.

The receptaculum seminis is rather club-shaped and has a short duct. It is surrounded by a muscular layer. The cells are columnar with basal nucleus and their structure

seems to indicate a glandular nature. Very occasionally spermatozoa were found in the receptaculum aggregated into small subcircular clumps.

(2) The Oviducal and Accessory Glands.

Some excuse is perhaps required for cumbering nomenclature with an additional obscurity. The appendage (Text-fig. 9) borne upon the oviduct just below the receptaculum seminis is called by Seibold the 'Anhangsdrüse des Receptaculum seminis' and by Bregenzer the 'Eiweissdrüse'. The latter's figures are not a sufficient indication whether structurally the organs are similar in *Bythinella* and *P. ventrosa*. Devoting our attention to the latter we find the 'oviducal gland', as I prefer to call it, to be covered by a strongly-developed muscular sheath with circular muscle fibres. In general form it is an irregular-shaped gland with a short duct. Internally it is very much folded. The cells of its inner layer when not loaded with secretion are tall and narrow. The nuclei are basal, and, when the cells are full of secretion, they become driven close up against the basal membrane. There are not very many accounts of the albumen gland in Gastropoda. But from those available we can safely assume that we are hardly warranted in calling this structure in *Paludestrina* by that name. In *Valvata* (1) on the one hand and *Physa* (22) on the other we see radically different types of 'albumen gland', and we can identify this form with neither.¹ Until more is known of this structure in Gastropoda, and particularly in Prosobranchia, it is perhaps better to avoid a too positive terminology.

The vagina is a narrow slit-like cavity surrounded by a large accessory glandular mass. It is thin-walled and ciliated internally. The glandular mass is very interesting but difficult to interpret. Previous authors of recent work upon *Taenioglossa* do not discuss it at any length, though Seibold pointed out that differences of staining could be observed in it. Subject to certain qualifications, we may state that this mass is divisible most

¹ Cf. Slugoeka's Pl. iv, fig. 20.

frequently into two parts which occupy more or less opposite sides of the vagina and, where they meet, show a certain amount of transition in their structure.

One portion is usually stained in haematoxylin and eosin a vivid light purple in which the pink tinge predominates. It consists of two kinds of cells. A layer of ciliated, cubical cells lines the cavity of the gland. Some of them are drawn out into irregular, elongate extensions with which are associated other rather elongate cells. These form irregular digitiform glandular masses. A distinct lumen is seen in these masses (Text-fig. 10). It is uncertain how they pass their secretion to the exterior, as I have never observed a communication between the lumen and the exterior. The second area usually stains a deep purplish blue with the same stain. Seen in its most characteristic form it is composed of the same columnar ciliated cells and an inner glandular mass. The latter is more compact, the nuclei of the constituent cells are fewer and often arranged at the periphery of rudely quadrate masses. One is tempted to conclude that this second portion only represents another stage of the condition observed in the first described part, and that in the one the cells are full of secretion and tend to obscure a structure like that described in the first case. In the compact portion it is very hard to make out cell outlines, and certainly nothing like the digitiform glandular processes can be seen. It is, on the other hand, very certain that in certain areas transitional masses are to be found.

I am inclined on the whole to consider that there are two functionally distinct portions of this gland mass, though intermediate stages are found. A comparison may be made with the rather similar structure of the accessory glands (oötype, shell-gland, &c.) of Neritacea which have been described by Bourne (3).

The cavity of the vagina is continuous with those of the glands.

(3) Male Organs (Text-fig. 11).

The testis consists of a number of branching follicular tubes and in general plan resembles the ovary. Only one kind of

spermatozoon was found, viz. the 'typical'. The definitive stage of the latter, which is found in the vas deferens and the receptaculum seminis of the female, exhibits an elongate conical 'head', a usually well-developed acrosome, an acute apical portion, no discernible middle-piece, and an elongate tail. The precise length of the latter could not be very satisfactorily ascertained, but it is apparently very much longer than that of *Bythinella*, in which the tail is between twice and thrice as large as the head. In *P. ulvae* and *P. taylori* (Robson MS.) the tail is relatively enormous. One of the constant features of spermatogenesis is the occur-

TEXT-FIGS. 11-12.

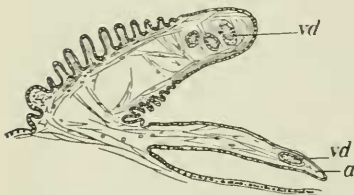


Fig. 11.—Section of penis. *a*, free portion of 'appendage'; *vd*, vas deferens.

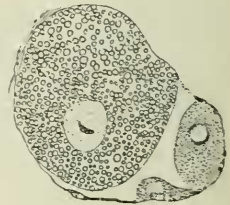


Fig. 12.—Transverse section through ovarian follicle.

rence in the spermatids of an arrangement of the chromatin of the nucleus in bent rods or half-hoops at the periphery of the nucleus. My friend Dr. J. B. Gatenby has pointed out to me the rather similar concentration of chromatin at the posterior part of the nucleus in the spermatid of *Murex trunculus* recorded by Schitz (19). I am also indebted to Dr. Gatenby for pointing out to me the frequent occurrence of abnormal stages of spermatocytes, though of course, as has been stated above, the spermatozoa are monotypic.

The vas deferens is thin walled during the first part of its course. It passes down the columellar region and in the neighbourhood of the kidney gives rise to a large glandular swelling, the prostate. The latter has plicate walls in-

teriorly, lined with columnar ciliated cells with more or less basal nuclei. The rest of the structure of this gland, which stains violet with haematoxylin and eosin, is not unlike that of the lighter-staining portion of the accessory gland of the female.

Below the prostate the vas deferens becomes smaller, thick-walled, and ciliated. It eventually runs just below the epidermis in the floor of the pallial cavity to the penis, which it traverses up to its apex. The penis is single in contrast with the remarkable complexity of *Bythinella* and *Bythinia* (Moquin Tandon, 13), in which a flagellum and a second branch occurs. It therefore exhibits the condition seen in *Cyclostoma* (Garnault) and *Vitrella*. In *P. ulvae* the penis is quite simple according to Henking, while drawings made from the living animal by my friend Dr. H. Quick also show no accessory structures upon the male organ. The intromittent portion in *P. ventrosa* is long and pointed.

3. HABITS, ETC.

A preliminary attempt has been made (Robson, 17) to analyse the ecological conditions under which *P. ventrosa* is found. But a great deal remains to be done upon this subject as well as upon the distribution and ecology of the plants associated with it and upon which it may be presumed to depend. Though a more definitely brackish-water form than *P. ulvae*, the case worked out at Leigh-on-Sea demonstrated a greater adaptability and tolerance on the part of *P. ventrosa*. If, as we may rightly assume, the British Paludestrinidae show a progressive tendency to become adapted to fresh-water, *P. ventrosa* represents an intermediate stage of adaptation, but exhibits the tendency in its initial rather than its later stages. Little can be said upon the more intimate habits of this animal. It is usually found upon some water-plant, but quite frequently upon mud or bottom débris. In several examples from Leigh, Wakering Wick, and elsewhere, the stomach contained a variety of diatoms and a few foraminifera.

fera. The rest of the contents were usually too much digested to enable their nature to be made out. No remains of plant fibre, &c., was ever found. I am inclined to think that it browses upon the microfauna and microflora of the plants upon which it lives, and that it does not actually chew the leaves of the latter.

4. AFFINITIES.

(a) I cannot agree with Bregenzer's verdict upon the immediate relationships of *Paludestrina* (6, p. 276). According to her, the latter genus is separated into a group distinct from *Bythinella* and *Vitrella* upon the following characters :

- (1) Fusion of the cerebral and pleural ganglia.
- (2) The possession of two pairs of salivary glands.
- (3) Reduction of the 'Knorpelspange' of the lingual cartilages.
- (4) Brackish-water habitat.

Of these characters the first is open to question. In *P. ventrosa* there is no more fusion of the ganglia in question than in *Bythinella*, while in *P. ulvae* we have seen (p. 168) that Henking's statements are open to question. In the second place, only one pair of salivary glands is found in *P. ventrosa*. As to the third character it is scarcely worth anything as the 'Knorpelspange' is absent in *Vitrella*! Lastly, *Paludestrina* is not restricted to brackish water, at least as far as England is concerned. As the result of a scrutiny of the characters available for taxonomic purposes we might with equal justification select the simple penis and longer super-intestinal part of the visceral commissure in order to unite *Paludestrina* with *Vitrella* as against *Bythinella*, or the crystalline style and certain features of the radula to unite *Paludestrina* and *Bythinella* against *Vitrella*. In any case I venture to think that an animal's taxonomic position cannot be summarily decided in this fashion. Until we have objective evidence as to the taxonomic value of the various characters such groupings as those discussed above are of little value. On the whole we can safely consider these

genera as referable to the same family ; but I feel that we require another technique for deciding their closer affinities than a mere inspection and assorting of characters. A character such as the absence of the crystalline style in *Vitrella* would appear in the first instance to be profoundly important. But we do not know the precise significance of its absence.

As an alternative to a close study of genetics, evolution, habits, and ecology in relation to structure which alone can give us a sound taxonomic method, the only procedure that could be suggested would be a complete enumeration of characters and a grouping based upon agreement or disagreement in a large number of structures. This method would be crude, but it would be better than an arbitrary selection of a few characters. In the present case I have distinguished a total of twenty-one important characters. The agreement or disagreement of the three genera in question is indicated as follows :

Paludestrina=	Bythinella alone in	5
„	= <i>Vitrella</i> alone in	2
„	= <i>Bythinella</i> and <i>Vitrella</i> in	4 21
„	=neither in	8
	relationship uncertain in	2

(b) Though it would be beyond the scope of this paper to offer a criticism of the present arrangement of the *Taenioglossa*, we may nevertheless attempt to define the position of the *Paludestrinidae* with regard to some of the main tendencies of *Prosobranch* morphology.

The *Paludestrinidae* represent a stage in the abbreviation of the nervous system which involves the pleural-intestinal portions, and is seen in its extreme condition in *Bithynia* and *Valvata* in which the sub- and supra-intestinal ganglia are either fused or closely approximated to the pleural ganglia. In *Melania* and *Cerithium* this condition of close approximation is seen on one side only, the ganglia being separated on the other side. In *Paludestrina* and *Bythinella* they are slightly separated on both sides, while in *Littorina* and *Paludina* they are widely separated.

Paludestrina agrees with *Pterocera*, *Tiphobia*, *Lithoglyphus*, and a few others in possessing a crystalline style. We may assume, however, that this is without phylogenetic significance within the group.

Another interesting tendency which may not be of phylogenetic importance is the possession of a single otolith in the *Paludestrinidae*. It shares this character with *Littorina*, *Truncatella*, some *Melantias*, and *Natica*. On the other hand, *Paludina*, *Ampullaria*, *Valvata*, *Cyclophorus*, and others have multiple otoconia. A blood-gland is absent from the kidney of *Paludina*, *Valvata*, *Cerithium*, &c., and is found in *Littorina* and in the *Paludestrinidae*.

Finally, while possessing a simple osphradium, *Paludestrina* exhibits a definite osphradial ganglion—a stage apparently more advanced than such forms as *Littorina* and *Bithynia*, in which (Bernard, 2) no osphradial ganglion is found.

5. SUMMARY.

1. *Paludestrina ventrosa* possesses the general Taenioglossate organization.
2. It represents a genus of *Paludestrinidae* equivalent to *Bythinella* and *Vitrella*.
3. It is peculiar within the family as possessing :
 - i. Folded gills ;
 - ii. A slit connecting the style sac through nearly all its length with the intestine ;
 - iii. A typhlosole ;
 - iv. A non-ciliated roof to the median part of the pharynx.

It represents an intermediate stage in the acquirement of the fresh-water mode of life, being essentially a brackish-water form with a fairly well-marked euryhaline tendency.

4. Several structures not fully described by previous authors are discussed in this paper (e.g. the accessory female and circulatory organs), and it is not certain in what form these structures occur in other Taenioglossa.

5. Within the Order Taenioglossa, Paludestrina is referable to the group which possesses :

- (1) a brevicommissurate visceral commissure ;
- (2) a single otolith ;
- (3) an osphradium with basal ganglion ;
- (4) a renal-portal system and blood-gland ;
- (5) an 'oviducal' gland immediately adjacent to the receptaculum seminis.

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